PALÆO VERTEBRATA

First Neogene *Otonycteris* (Chiroptera: Vespertilionidae) from Ukraine: its biostratigraphic and paleogeographic significance

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Abstract: A new species, *Otonycteris rummeli* nov. sp., is described from the Late Miocene site Gritsev (MN 9) in the Ukraine. *Otonycteris rummeli* nov. sp. differs from those of most vespertilionids, except recent *Otonycteris*, *Antrozous* and Early Miocene *Karstala silva*, in having a well-developed entocingulid at the foot of the trigonid valley in the lower molars. The morphological resemblance of *Otonycteris*, *Antrozous* and *Karstala* is apparently a case of convergence in the evolution of the Old and New Worlds bat faunas. From at least the Middle Miocene the range of *Otonycteris* distribution spread to the whole of Central Europe and such a situation continued during the whole Late Miocene. This indicates a more arid climate in Europe during the Upper Miocene compared to the Quaternary. The reduction of the distribution range of *Otonycteris* and its extinction in most of the territory of Europe could have been caused by the global climatic cooling and increasing glacial cycle amplitude during the onset of the Quaternary.

Keywords: Mammalia, bats, Late Miocene, Gritsev, East Europe

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INTRODUCTION

Bats of the genus *Otonycteris* Peters, 1859 are the largest vespertilionids in their range (Gharaibeh & Qumsiyeh, 1995). Recent species of this genus have long prominent ears but not as long as those of *Plecotus* long-eared bats, together with which they are placed within the tribe Plecotini (Benda & Gvoždík, 2010; Roehrs *et al.*, 2011). The members of the tribe Plecotini are widely distributed throughout the Northern Hemisphere and include the Palearctic genera *Barbastella, Plecotus* and *Otonycteris* and the Nearctic genera *Corynorhinus, Idionycteris* and *Euderma*. According to both a morphological study (comparisons of cranial and bacular characters) and molecular genetic comparisons of mitochondrial genes, two separate species, *O. hemprichii* sensu stricto (that inhabits North Africa and Middle East) and *O. leucophaea* (Severcov, 1873) (that inhabits Central Asia), are currently recognised within the genus *Otonycteris* (Benda & Gvoždík, 2010). Within *O. hemprichii* sensu stricto, three separate subspecies were found: *O. h. hemprichii* Peters, 1859 (that inhabits North Africa, Levant and Mesopotamia), *O. h. cinerea* Satunin, 1909 (that inhabits mountainous areas of eastern Arabia and Iran) and *O. (h.) jin* Cheesman & Hinton, 1924 (that inhabits lowland deserts of eastern Arabia and south-eastern most Iran; Benda & Gvoždík, 2010).

Fossil *Otonycteris* are very rare. Until recently only two records of this genus are known from the Miocene localities of France: La Grive M (MN 7, Mein & Ginsburg, 2002) and Soblay (MN 10, Ménouret & Mein, 2008). From the Late Miocene site Mytilini (Samos, Greece; Forsyth Major, 1892) is known the articulated skull of the *Samonycteris majori* Revilliod, 1922 which is morphologically close to the genus *Otonycteris* (Revilliod, 1922), but differs from it in certain cochlear features (Horáček, 1991). Other Late Miocene bat taxa, known only from dentaries and isolated teeth determinate as aff. *Samonycteris* (Suchomasty 3, MN 9, Czech Republic; Horáček, 2001) and *Scotophilus*? (Steinheim, MN 7, Germany, and Anwil, MN8, Switzerland; Engesser, 1972) could belong to the same phylogenetic clade (Horáček *et al.*, 2006: pp. 136).

New discoveries of the fossil *Otonycteris* from the Early Vallesian locality of Gritsev in the Ukraine (MN 9; Vangengeim *et al.*, 2006) are presented in this work. Stratigraphy, taphonomy and vertebrate fauna of the Gritsev locality are well-known (Topachevsky *et al.*, 1996; Nesin & Kowalski, 1997; Rzebik Kowalska & Topachevsky, 1997; Morlo & Semenov, 2004; Vangengeim *et al.*, 2006). The fossil bat fauna from the Gritsev site is very rich and diverse; some new vespertilionid bats have already been described (Rosina & Semenov, 2012). The morphological peculiarities of the new fossil *Otonycteris* species from the Gritsev site propose new perspectives on bat paleogeography and the biostratigraphical distribution of this genus.

MATERIAL AND METHODS

The fossil material of the *Otonycteris* from Gritsev is represented only by dentary fragments and isolated teeth. Dental terminology generally follows that of Miller (1907) with the addition of the entocingulid (Hutchinson, 1974). An accepted specific nomenclature for upper bat canines does not exist and here we use our own variant (see Fig. 1) combined with that of Freeman (1992). The tribe taxonomy follows Simmons (2005). Measurements were made with a binocular microscope MBS-10 calibrated with a stage micrometer. All measurements of fossils are in mm. Lengths of individual teeth and tooth-rows were taken as the maximal distances between the posterior and anterior crown edges of the respective teeth. Tooth widths were taken as the maximal distances between the lingual and buccal crown edges. The heights of the C sup. and C inf. are measured lingually. The following measurements (in mm) were taken:

length (L) × width (W) × height (H) of C inf., C sup., p4, (in the case of p4 – the maximal width of the p4 crown); length × width of the molar trigonid (Wtr) × width of the molar talonid (Wtl) of m 1,2,3; length of the m3 talonid (Ltlm3); lengths of the tooth-row: Lm2-3; Hmdm3 – the height of a mandibular corpus measured from the lingual side below m3. The following abbreviations and abridgements were used in a text: sup. – superior; inf. – inferior.

The fossils described here are from the vertebrate paleontology collection of the Palaeontological Museum of the National Museum of Natural History, National Academy of Sciences of the Ukraine (NMNHU). The osteological collections of recent Chiroptera, deposited in the Palaeontological Museum and in the Zoological Museum of the NMNHU, in the Zoological Museum of Moscow University (Moscow, Russia) and in the Senckenberg Research Institute (Frankfurt-am-Main, Germany), have been used for the comparisons. The photographs have been taken with a scanning electron microscope of the Borissiak Paleontological Institute of the Russian Academy of Science.

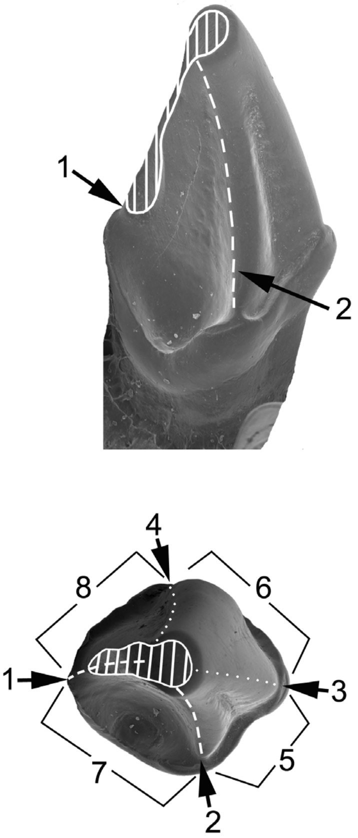

Figure 1. Nomenclature for the bat upper canines used in this study combined with that of Freeman (1992). The photos of the upper canine of *Otonycteris leucophaeus* (S-103165, coll. ZMMU); (1) lingual view, the occlusal view (2) is positioned such as the tooth sitting in the tooth row. The white broken line traces the path formed by the crests and the white dashed line traces the path formed by the ridges of the canine crown. The shaded region traces the occlusion mark on the crown.

1 – posterior crest (= "premolar-directed edge" of Freeman, 1992, or eocrista of Hershkovitz, 1971) descending from the posterior portion of the cingulum all the way to the apex;

2 – lingual crest (= "incisor-directed edge"; Freeman, 1992), which descends the lingual side of the crown to the apex;

3 – anterior ridge (= "labial edge", ibid.) extends at the anteriormost side of the crown;

4 – buccal crest descending from the buccal side of the crown to the apex;

5 – anterolingual face – the area between the anterior ridge of the crown and the lingual crest.

6 – anterobuccal ridge (= "bulge or torus", ibid.) extends between the anterior ridge and the buccal crest;

7 – posterolingual concavity (= "lingual edge" of Freeman, 1992 or longitudinal concavity of Ziegler, 2003) extends between the posterior and lingual crests;

8 – posterobuccal face – the area between the buccal and posterior crests.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order CHIROPTERA Blumenbach, 1779
Family VESPERTILIONIDAE Gray, 1821
Tribe PLECOTINI Gray, 1866

Otonycteris Peters, 1859
(Fig. 2-3)

Type species. *O. hemprichii* Peters, 1859.

Included species. *O. hemprichii* Peters, 1859, *O. leucophaea* (Severcov, 1873).

Range and distribution. Recent species are distributed in most arid and semiarid areas of the central and South-Western Palaearctic from Morocco, Southern Algeria and Niger to Egypt and Sudan; and over the whole Middle East and Central Asia to Afghanistan and northwestern India (Benda & Gvoždík, 2010). Fossils of this genus are reported only from the Middle and Late Miocene of France from the sites La Grive M (MN 7, Mein & Ginsburg, 2002) and Soblay (MN 10, Ménouret & Mein, 2008).

Diagnosis. Gharaibeh & Qumsiyeh, 1995. *Otonycteris* are the largest vespertilionids in their geographic range. The skull is large and similar to that of a large *Eptesicus* or *Myotis* with robust teeth. The dental formula is i 1/3 c 1/1 pm 1/2 m 3/3, total 30. M3 is greatly reduced, without a metacone or mesostyle.

Otonycteris rummeli sp. nov.

Holotype. Ch/350, a right dentary fragment with m2-3 (Fig. 2 A).

Hypodigm. (measurements see Tabl. 1 and 2). The holotype and Ch/88 (left m1), Ch/301 (right C sup.), Ch/347 (left C inf.), Ch/348 (left p4), Ch/349 (left m3), Ch/383 (right proximal fragment of dentary with alveoli of m3).

Measurements of the holotype. Lm2-3 4.40; m2 2.55 × 1.60 × 1.60; m3 2.08 × 1.35 × 0.60, Ltlm3 0.70; Hmdm3 3.00.

Type locality. Gritsev, near the village of Hrytsiv, Shepetivskii district of the Khmelnitskii region, Ukraine.

Age. MN 9, the Bessarabian regional stage of the Late Miocene.

Etymology. The specific name is given in honour of Dr. Michael Rummel from Weißenburg, Germany, my partner and beloved spouse, who enthusiastically supports my researches of fossil bats.

Differential diagnosis. Differs from most vespertilionids in having an entocingulid (for details see below) in the lower molars. Differs from *Antrozous* in its larger size, in having a

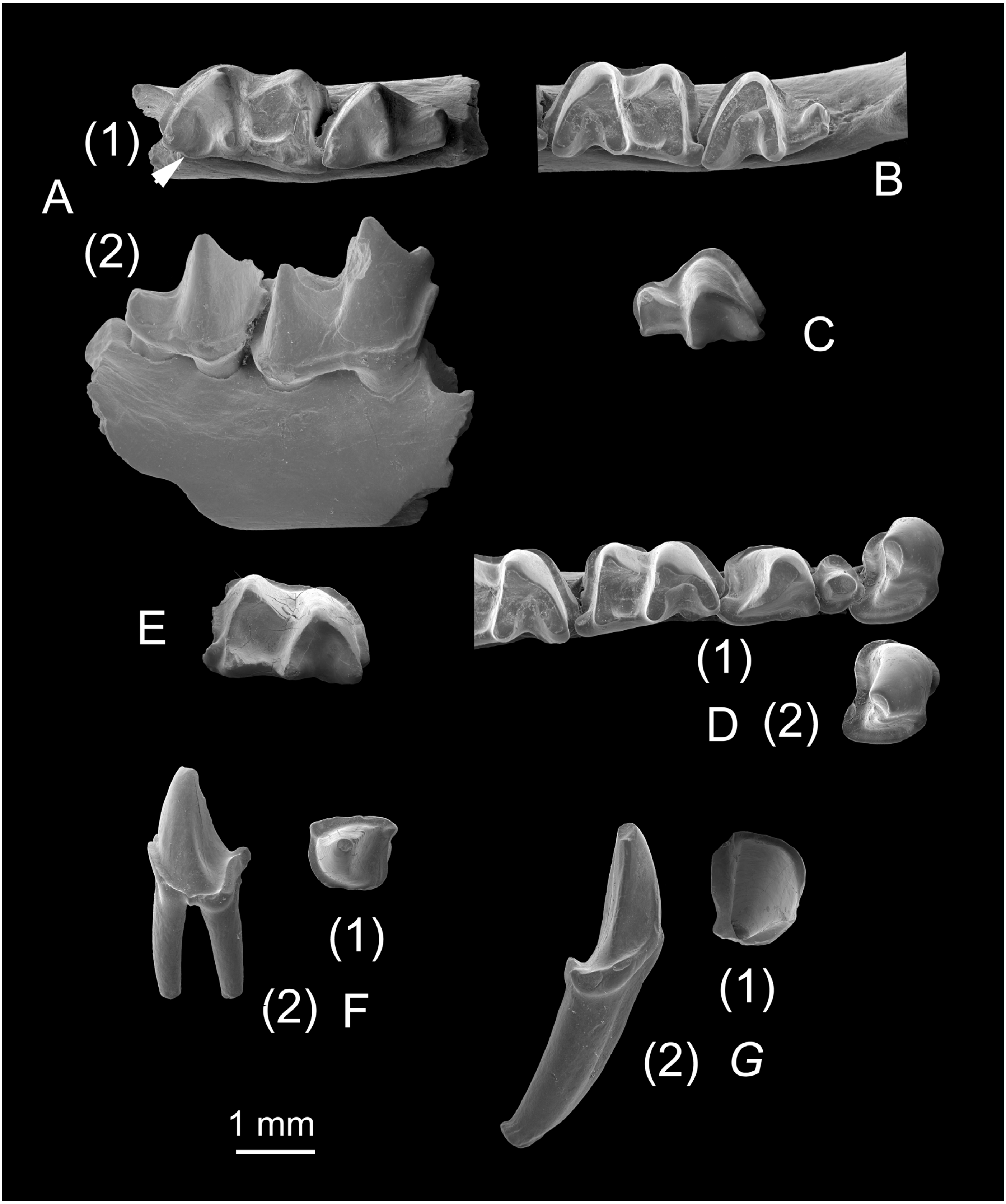

Figure 2. A, C, E, G *Otonycteris rummeli* sp. nov.: **A,** right dentary fragment with m2 and m3, holotype, Ch/350 (1) ventral view, (2) lateral view; **C,** left m3, paratype, Ch/349 occlusal view; **E,** left m1, paratype, Ch/88 occlusal view; **F,** left p4, paratype, Ch/348, (1) occlusal view, (2) buccal view; **G,** left C inf., paratype, Ch/347, (1) occlusal view, (2) lingual view. The white arrow sign marks the entocingulid in lower molars.
B, D *O. leucophaeus* S-103165, coll. ZMMU: **B,** right proximal part of dentary with m2 and m3, ventral view; **D,** (1) left distal part of dentary with C inf.-m2, (2) left C inf., occlusal view.

	Ia io recent, Thailand	***Otonycteris rummeli*** **nov. sp., Late Miocene, Ukraine**	*Eptesicus serotinus* recent, Ukraine, Yugoslavia	*O. leucophaea*, recent, Central Asia	*O. hemprichii* s. str., recent, Africa	*Samonycteris majori*, Mytilini, Samos, Late Miocene	*Myotis myotis*, recent, Eastern Europe	*Scotophilus*?, Late Miocene, Switzerland	*Scotophilus*?, Late Miocene, Germany	*Antrozous pallidus*, recent and Pliocene, North America	*Karstala silva*, Early Miocene, North America
n	-	**6**	2	3	1	1	2	8	1	-	7
LC inf.	1.80	**1.40**	1.50	1.33-1.77 (1.53)	1.43	-	1.20	-	-	1.01-1.05 (1.03)	-
WC inf.	1.95	**1.70**	1.58-1.70	1.58-1.67 (1.63)	1.58	-	1.35-1.50 (1.43)	-	-	1.28-1.31 (1.29)	-
HC inf.	3.30	**>3**	2.60-2.92	2.83-2.93 (2.89)	2.55	-	-	-	-	≈1.88	-
Lp4	1.58	**1.38**	1.33-1.40	1.48-1.67 (1.58)	1.54	1.40	1.50-1.55 (1.53)	-	-	1.05-1.13 (1.09)	-
Wp4	1.58	**1.23**	1.13-1.25	1.21-1.25 (1.23)	1.24	-	1.20-1.30 (1.25)	-	-	1.05-1.09 (1.07)	-
Lm2-3	4.95	**4.40**	3.30	4.08-4.33 (4.21)	3.86	-	-	-	-	3.23-3.56 (3.39)	-
Lm1	2.70	**2.58**	2.08-2.30	2.10-2.14 (2.12)	2.03	2.20	2.20-2.30 (2.25)	2.08-2.12 (2.11)	2.24	1.73	2.20
Wtrm1	1.58	**1.48**	1.20-1.21	1.05-1.16 (1.11)	1.01	-	1.30-1.45 (1.38)	-	-	0.90-0.94 (0.92)	1.25
Wtlm1	1.80	**1.65**	1.38-1.50	1.24	1.28	-	1.55-1.70 (1.63)	1.64-1.76 (1.62)	1.44	1.09-1.16 (1.13)	1.46
Lm2	2.70-2.83	**2.55**	2.08-2.20	2.19-2.38 (2.29)	2.10	2.20	2.40-2.45 (2.43)	2.20-2.24 (2.23)	2.24	1.70-2.04 (1.87)	2.18-2.22 (2.20)
Wtrm2	1.65	**1.60**	1.17-1.20	1.42-1.59 (1.50)	1.24	-	1.50	-	-	1.09-1.20 (1.15)	1.15-1.32 (1.27)
Wtlm2	1.95	**1.60**	1.38-1.45	1.50-1.58 (1.53)	1.35	-	1.75	1.64-1.70 (1.67)	1.50	1.13-1.30 (1.25)	1.25-1.50 (1.36)
Lm3	2.25	**2.03-2.08 (2.05)**	1.75-1.85	1.92-2.00 (1.97)	1.88	-	2.00-2.25 (2.13)	1.68-1.80 (1.74)	-	1.50-1.90 (1.72)	1.88
Wtrm3	1.50	**1.35-1.45 (1.40)**	1.17-1.20	1.39-1.46 (1.42)	1.20	-	1.40-1.50 (1.45)	1.56-1.66 (1.61)	-	0.98-1.11 (1.06)	1.35
Wtlm3	1.13	**0.60-0.80 (0.70)**	0.79-0.80	0.67-0.71 (0.70)	0.68	-	0.90	-	-	0.53-0.60 (0.57)	0.9
Ltlm3	1.05	**0.70**	0.75	0.66-0.75 (0.72)	0.60	-	-	-	-	0.45-0.64 (0.54)	-
Hmdm3	3.30	**3.00-3.20 (3.10)**	2.67-2.90	2.72-3.33 (2.99)	2.78	2	2.65-3.20 (2.93)	-	-	2.25-2.40 (2.33)	≈2.6
References	own data, Czaplewski & Morgan, 2000	own data	own data	own data	own data	Revilliod, 1922	own data	Engesser, 1972	Engesser, 1972	own data, Thewissen & Smith, 1987	Czaplewski & Morgan, 2000

Table 1. Comparison of dentaries of *Otonycteris rummeli* nov. sp. from Gritsev with those of some fossil and recent vespertilionid bats (in mm, the size difference between maximum and minimum values, an arithmetic mean is in brackets; n – number of specimens).

less lingually displaced, more labially situated hypoconulid and entoconid aligned with paraconid-metaconid, particularly in m1, and in having a well-developed mesolingual cingular cuspid in C sup. and an elongate p4 which has smaller anterior and posterior tubercles at the lingual side of the crown. Differs from *Samonycteris majori* in having larger lower molars and in an appreciably difference in shape of C sup. Differs from *Karstala silva* Czaplewski & Morgan, 2000 in being larger, in having an evident hypoconulid in m3 and in better developed mesolingual and posterolingual cingular cuspids in the upper canine. Differs from recent *Otonycteris* species in its larger size, in having a more developed entocingulid in m2 and a less reduced talonid in m3, in a more roundish occlusal view of C sup. Differs further from *Otonycteris* in its smaller paraconids in the lower molars which do not extend lingually beyond the tooth outline and in its shorter paracristids in m2-3.

Description

The holotype is a proximal part of a horizontal ramus with only the crowns of m2 and m3; it is broken in front of the m2 and with a broken ascending ramus (Fig. 2 A). The dentary is robust and very large. The hypoconulid of m2 is well-marked and situated rather labially to the entoconid. The talonid of m3 is appreciably reduced. In m3 of the holotype the hypoconulid is almost indistinguishable, however in m3 of the paratype specimen (Ch/349) the hypoconulid is visible (Fig. 2 C). The paraconid is the most developed conid on the lower molars. In m1 (specimen Ch/88) and m3 (specimens Ch/349, 350) it is displaced lingually but not in m2 (specimen Ch/350, Fig. 2 A, C, E). The talonid of m1 and m2 is barely wider than the trigonid (Fig. 2 A, E; Tabl. 1). The angle formed by the paracristid and protocristid in m1 is wider than in m2 (specimens Ch/88 and Ch/350). In lower molars the paracristid is barely curved and longer than the protocristid (to a lesser degree in m1). The molars are myotodont and have a small crest (entocingulid of Hutchinson, 1974: Fig. 1b; or "lingual cingulid" of Czaplewski & Morgan, 2000; or "metacristid" of Menu, 1985: Fig. 2) at the foot of the trigonid valley on the anterolingual base of the metaconid, which extends steeply downward and forward to the posterolingual base of the paraconid (Fig. 2 A (1)). This short cingulid crest encloses a moderately deep groove that is confluent posteriorly with the trigonid valley. The entocingulid is pronounced in m2 whereas it is more weakly defined in m1 and m3 (Fig. 2 A, C, E).

The isolated teeth (canines and p4) are assigned to the new *Otonycteris* species on the basis of their large size. The lower canine (Fig. 2 G) is crescent-shaped in occlusal view and surrounded by a well-developed cingulid, the anterolingul part of which gradually turns into the main cone of the tooth without forming an anterolingual cuspid. It has a root volume appreciably larger than that of the crown (Fig. 2 G). The p4 is triangular in occlusal view (Fig. 2 F) and surrounded by a distinct cingulid which forms small anterior and posterior tubercles at the lingual side of the crown. The two roots of p4 are equal to one another in size.

The upper canine is very large and robust; the volume of the root is somewhat greater than that of the crown (Fig. 3 A). It is somewhat diamond-shape in occlusal view and has a well-developed undulating cingulum which is narrow labially and broad lingually. It has an appreciable rise posterolingually and forms a well-developed mesolingual cingular cuspid. The crown has a sharp posterior crest descending from the posterior portion of the cingulum all the way to the apex, and a lingual crest which is less sharp and descends down the medial side of the crown to the apex. Between these two crests is a broad posterolingual concavity. The area between the anterior ridge of the crown and the lingual crest is slightly concave and narrow. The anterobuccal ridge of the crown is convex and smoothly rounded.

Comparisons

According to a myotodont configuration of the lower molars and a well-developed cingulum of the crowns, the fossil specimens from Gritsev belong to the family Vespertilionidae. All fossil remains are very large and correspond to each other in sizes.

The upper canine of *Otonycteris* from Gritsev is edged (specimen Ch/301, Fig. 3 A) and not simply round or oval as that of large *Myotis* species, e.g. *Myotis myotis*. However, it is more roundish in cross-section and does not have an anterolingual narrow thickening of cingulum in comparison to the upper canine of *Vespertilio*. In addition, it is also more roundish and has no second tip on the cutting edge of the upper canine as in *Nyctalus*. The upper canine from Gritsev is somewhat similar to that of the Late Miocene molossid *Meganycteris monslapidis* Rachl, 1983 (Steinberg, Goldberg, MN 6, Germany), which is also very large in size. Nevertheless, the Gritsev specimen is smaller (Tabl. 2) and differs from *M. monslapidis* in having more rounded cross-sectional shapes of both the root and the tooth crown and in having a more developed mesiolingual cingular cuspid (Fig. 3 A; Rachl, 1983: 134, Fig. 47). The upper canine from Gritsev is also close in size to those of large *Eptesicus*, e.g. *E. serotinus* (Tabl. 2). However, in contrast to the upper canines of most *Eptesicus* species, which are diamond-shaped in occusal view, the upper canine from Gritsev is more roundish and not so compressed in the buccolingual direction as that of *E. serotinus.* Furthermore, the upper canine of *E. serotinus* has no mesolingual cingular cuspid and its anterolingual face is narrower than in the fossil canine from Gritsev. Similar differences exist between the upper canine from Gritsev and that of the recent large vespertilionid *Ia io* (see also Tabl. 2). The upper canine of the Miocene *E. campanensis* is also roundish in occusal view, similar to the fossil canine from Gritsev, and it has the same rate LC/WC×100% <120 (see Tabl. 2). But as distinct from the Gritsev specimen, it has a less developed mesolingual cingular cuspid and a narrower anterolingual face of the crown (Baudelot, 1972: 70, Fig. 27; Ziegler, 2003: 462, Fig. 3.1; Rosina & Sinitsa, 2014: 156, Fig. 3H).

The fossil canine from Gritsev is very close in size to the upper canine of *Samonycteris majori* (Tabl. 2), but, as Horáček asserts, they appreciably differs in shape (pers. comm. Horáček; Revilliod, 1922: Fig. 52-54, pp. 142; Horáček, 1991; Horáček, *et. al.*, 2006: Fig. 4, pp. 139).

The shape of the upper canine of recent *Antrozous* is very similar to that of the fossil canine from Gritsev, especially in the width of the anterolingual face of the crown, which is considerably less than in the canine of recent *Otonycteris*. However, as distinct from the fossil canine from Gritsev the recent *Antrozous* has no appreciable mesolingual cingular cuspid in the canine crown. For differences from *Karstala silva* see the Differential diagnosis above.

Similar to the upper canine of recent *Otonycteris* the upper canines from Gritsev have a well-developed cingulum, which becomes thin between the posterior and lingual crests and forms a posterolingual concavity of the crown. But the concavity is deeper and more extended in the recent species (Fig. 3 A, B). Furthermore, the upper canines of recent *Otonycteris* have a more developed anterobuccal ridge and deeper concavity of the anterolingual face of the crown.

The lower canine from Gritsev (specimen Ch/347, Fig. 2 G) differs from that of the large *Myotis* species in being more compressed in the anteroposterior direction. It differs from the lower canines of *Nyctalus, Vespertilio Eptesicus* and *Ia* in missing an anterolingual cuspid. The lower canine of *Antrozous* is more compressed in the anteroposterior direction than the lower canine from Gritsev. By the shape the latter is very similar to the lower canines of recent *Otonycteris* (Fig. 2 D) and differs in being less compressed in the anteroposterior direction and in having a smaller posterolingual cingular cuspule on the crown.

The lower p4 from Gritsev (specimen Ch/348, Fig. 2 F) is more compressed in the anteroposterior direction than those of large *Myotis* species which have longer p4 crowns (Tabl. 1). On the other hand, the fossil p4 from Gritsev is not so

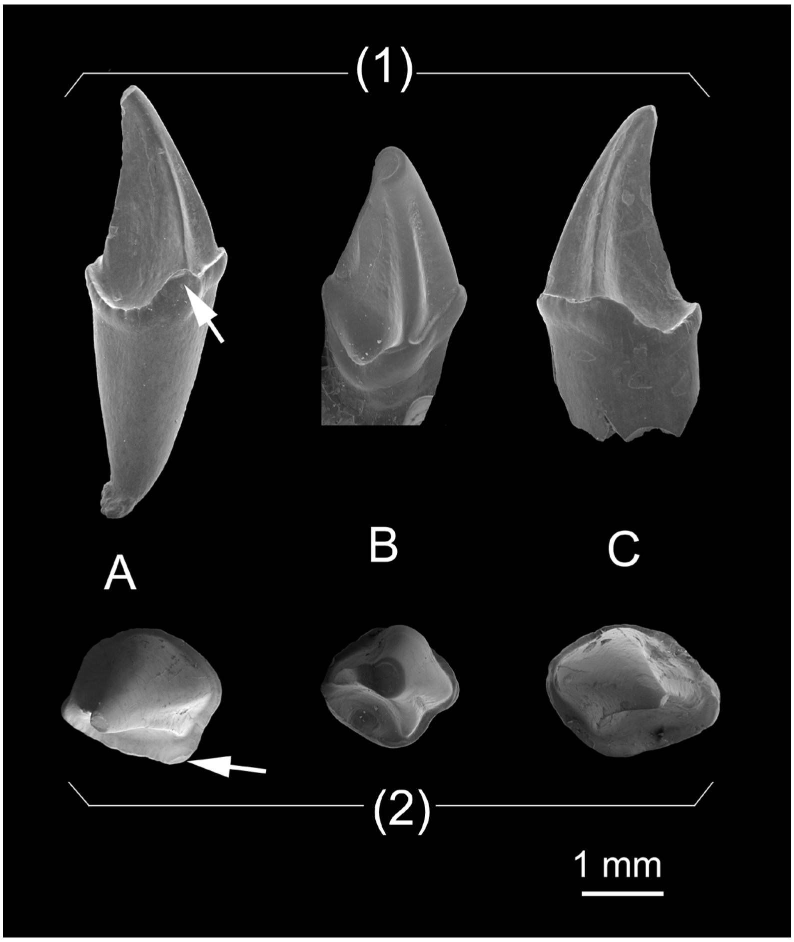

Figure 3. A, *Otonycteris rummeli* sp. nov. right C sup., paratype, Gritsev, Ch/301; **B,** *O. leucophaeus*, right C sup., S-103165, coll. ZMMU; **C,** cf. *Otonycteris* sp., left C sup., Gritsev, Ch/302; (1) lingual view, (2) occlusal view. The white arrow sign marks the mesolingual cingular cuspid.

	Meganycteris monslapidis, Goldberg, Middle Miocene, Germany	*Ia io,* recent, Thailand	cf. ***Otonycteris* sp.** Gritsev, Gritsev, Late Miocene, Ukraine	*Samonycteris majori* , Mytilini, Samos, Late Miocene	***Otonycteris rummeli*** nov. sp., Gritsev, Late Miocene, Ukraine	*O. leucophaea,* recent, Central Asia	*O. hemprichii* s. str., recent, Africa	*E. campanensis,* Petersbuch 10, Late Miocene, Germany	*E. campanensis,* Petersbuch 28, Early Miocene, Germany	*E. campanensis,* Petersbuch 6, Late Miocene, Germany	*E. campanensis,* Sansan, Middle Miocene, France	*E. serotinus,* recent, Ukraine, Yugoslavia	*Karstala silva* , Thomas Farm, Early Miocene, North America	*Antrozous pallidus* , recent, North America
n	-	1	1	1	1	3	1	2	1	1	2	2	1	2
LC	3.43-3.80	2.68	2.55	2.20	2.15	1.93-2.00 (1.98)	1.80	2.10-2.13	1.95	2.07	2.01-2.10	2.08-2.10	2.10	1.43-1.50 (1.46)
WC	2.75-2.85	2.24	1.90	-	1.90	1.63-1.74 (1.68)	1.50	1.93	1.70	1.77	1.87-1.96	1.58	1.85	1.24-1.35 (1.29)
HC	-	4.46	3.70	4.00	>3,8	2.37-3.67 (3.02)	3.30	3.62	3.40	>2.95	3.55	3.50	3.25	2.63
LC/WC×100%	-	119.6	123.1	-	113.2	110.9-123.1 (118.0)	120.0	110.4	114.7	116.9	107.2-107.5	131.6-132.9	113.5	111.1-115.2 (113.1)
References	Rachl, 1983	own data	own data	Revilliod, 1922	own data	own data	own data	Ziegler, 2003	Rosina & Rummel, 2012	Ziegler, 2003	Ginsburg & Mein, 2012; Boudelot, 1972	own data	Czaplewski & Morgan, 2000	own data

Table 2. Comparison of the upper canines of fossil *Otonycteris* from Gritsev with those of some fossil and recent bats (in mm, the size difference between maximum and minimum values, an arithmetic mean is in brackets; n – number of specimens).

strongly compressed as those of *Vespertilio* and *Nyctalus.* It differs from those of *E. serotinus* and *E. campanensis* in having a more roundish crown in the occlusal view (compare with *E. serotinus:* Horáček *et al*., 2006: 135, Fig. 2 (5b)) and with *E. campanensis:* Baudelot, 1972: Pl. II, Fig. 13). Thus, the lower p4 from Gritsev is most similar to the lower p4 of recent *Otonycteris* (Fig. 2 D) but a bit larger (Tabl. 1). It is also larger than the p4 of *Antrozous* (ibid.), besides which it differs in having smaller anterolingual and posterolingual cingular cuspules.

The lower molars from Gritsev differ from those of most vespertilionids, except *Otonycteris*, *Antrozous* and *Karstala silva*, by the presence of a well-developed, steeply inclined entocingulid at the foot of the trigonid valley (Fig. 2 A, C, E,). However, the lower molars of *Histiotus, Ia*, and *Hesperoptenus* also have a lingual cingulid that descends anteriorly from the metaconid, but very small and indistinct and furthermore it is frequently absent in m2. Also, a very small and indistinct lingual cingulid is present in the m1 of some large *Myotis* species, particularly *M. myotis* and *M. punicus* (Fig. 4), but it is almost indistinguishable in m2-3. Moreover, the lingual cingulid is also reported in *Barbastella, Corynorhinus* and *Quinetia* Horáček, 2001 and it is a typical feature of Plecotini (Horáček, 2001: pp. 136-137).

For the differences from *Antrozous* see the Differential diagnosis above. The images of recent and some fossil *Antrozous* species are set out in Freeman (1998: 149, Fig. 9.5A) and Thewissen & Smith (1987: 243, Fig. 3). *Anzanycteris anzensis* White, 1970 is known from the Late Pliocene localities LACM 6583 and LACM 6552 (Arroyo Seco local fauna) of California, USA, the lower cheek teeth of which "are essentially as in *Antrozous* and *Bauerus*" (White, 1970: 277). According to the illustration (White, 1970: 277, Fig. 4-5), the dentary fragment of *Anzanycteris* has a much reduced talonid in m3 like that of *Otonycteris* from Gritsev, but it is unclear if the entocingulids are present in the lower molars. In any case, *Anzanycteris* from California is much smaller than recent *Antrozous* (White, 1970: 279, Tabl. 2) and, respectively, smaller than *Otonycteris* from Gritsev. The same is with lower molars of *Samonycteris majori* from Samos which are appreciable smaller (Tabl. 1). According to the illustration (Engesser, 1972: Fig. 35b, pp. 125), the *Scotophilus*? from Anwil could have the entocingulid in m1, but the m3 of this species is smaller than that of *Otonycteris* from Gritsev (Tabl. 1). The same is with *Scotophilus*? from Steinheim (ibid.).

The lower molars from Gritsev differ from that of the fossil *K. silva* in being larger (Tabl. 1) and in having an entocingulid and an evident hypoconulid in m3 (specimen Ch/349, Fig. 2 C, Czaplewski & Morgan, 2000: 737, Fig. 1 H-I). Further difference from *K. silva* is better developed antero- and posterolingual cingular cuspids in the upper canine (specimen Ch/301, Fig. 3 A, Czaplewski & Morgan, 2000: 738, Fig. 2 A-E).

Recent *O. hemprichii* s. str. (Horáček *et al*., 2006: 137, Fig. 36 a, b) and *O. leucophaea* (Fig. 2) differ generically in the sizes of the tympanic bulla and in the positions of the basioccipital pits. In several aspects, e.g., in the size of the molars and molar-rows as well as the rostral widths across molars, they showed almost no significant differences (Benda & Gvoždík, 2010, our own data). However *O. hemprichii* s. str. is a bit smaller in size (Tabl. 1), and has a slender lower jaw. *Otonycteris rummeli* is larger in size then the recent species (Tabl. 1, 2) and differs in having a more developed entocingulid in m2 and a less reduced talonid in m3. The paraconids in the fossil molars are smaller and do not extend lingually beyond the tooth outline, and the paracristids in m2-3 are shorter than those of the recent *Otonycteris.*

Remarks

Besides the remains described here, only two other records of fossil *Otonycteris* are known. An isolated first upper molar defined as *Otonycteris* sp. indet. aff. *O. hemprichii* (Mein & Ginsburg, 2002) was reported from the Middle Miocene (MN 7) La Grive M site in France. A second fossil of *Otonycteris* sp. was described from the Vallesian locality Soblay (MN 10, France) and is represented by an isolated second upper molar (Ménouret & Mein, 2008). Comparison of the specimens under study with both of these remains was impossible. The same is with aff. *Samonycteris* (Suchomasty 3, MN 9, Czech Republic; Horáček, 2001), a single dentary of which is only illustrated in Horáček (2001: 149, Fig. 28).

The various dental elements of *O. rummeli* indicate that it was a relatively large vespertilionid, near in size to the larger known species of the family. No other bat in the Gritsev fauna approaches its size. *O. rummeli* is the largest vespertilionid bat so far discovered from the Tertiary of Eastern Europe.

cf. ***Otonycteris*** sp.

Fig. 3 C

Material (measurements see Tabl. 2)**.** Ch/302 (left C sup.).

Description

This upper canine is very large and very robust (Fig. 3 C). It is slightly diamond-shape in occlusal view and has a well-developed undulating cingulum which is narrow labially and broad lingually. The crown has an appreciable rise of cingulum posterolingually and a well-developed mesolingual cingular cuspid. The posterior and medial crests are sharp and they border a broad posterolingual concavity. The anterolingual face is slightly concave. The anterobuccal ridge of the crown is convex and smoothly rounded.

Comparisons

The cross section of this very large upper canine is more oval than that of the typical upper canine of the most recent *Eptesicus* species, which is diamond-shaped in occusal view. The crown of the fossil specimen from Gritsev is not so strong compressed in the buccolingual direction as that of *E. serotinus* or *Ia io*. Furthermore it differs from most *Eptesicus* and *Ia* in having a well-developed mesolingual cingular cuspid and a broader anterolingual face on the crown.

The fossil upper canine from Gritsev is similar to that of *Otonycteris,* particularly *O. rummeli* nov. sp., in having a well-developed mesolingual cingular cuspid and an appreciable rise of cingulum posterolingually. On the other hand, it differs from both recent and fossil *Otonycteris* in its much larger size (Tabl. 2), in its more oval-shaped crown and in its less prominent anterobuccal ridge (Fig. 3). The ratio LC/WC×100% is more than 120 (Tabl. 2) that corresponds more to a dental pattern of an *Eptesicus* canine.

Remarks

Given a considerable morphological difference between the upper canine of cf. *Otonycteris* sp. from Gritsev and the upper canine of *O. rummeli* (specimen Ch/301) it is also difficult to ignore their significant similarity (Fig. 3 A, C). The larger size of specimen Ch/302 in comparison to specimen Ch/301 of *O. rummeli* could have a biological meaning. It could be a case of a sexual size dimorphism that is very well documented among Vespertilionidae species, in which females are larger than males (Ralls, 1976; Myers, 1978; Schulz, 1999). Such reversed sexual dimorphism occurs in more lineages of mammals than is commonly perceived (Ralls, 1976). The differences are observed mainly in body weight, skull measurements and forearm length. Bogdanowicz & Owen (1996) found sexual size dimorphism in the skull of modern *O. hemprichii* using geometric morphometrics. Females are about 4.4% larger than the males (ibid.). Myers (1978) stated that bat females of Vespertilionidae are usually larger than males in order to provide a successful reproductive process. However, with respect to the remains of *Otonycteris* from Gritsev it is only an assumption due to the scarcity of fossils.

DISCUSSION

Odontological pattern of *Otonycteris* and its functional significance

Both fossil and recent species of *Otonycteris* ranks among the largest members of the family Vespertilionidae and are the largest plecotine bats. They are close in size to the large *Eptesicus serotinus*, *E. campanensis, Myoti*s *myotis*, to the Asiatic species *Ia io*, *I. lanna* Mein & Ginsburg, 1997 and *Hesperoptenus* (e.g. *H. tomesi* Thomas, 1905), and also to *Nyctalus lasiopterus*. Similar to all these large vespertilionids, *Otonycteris* is characterized by high-crowned teeth, especially the canines and last premolars. The upper molars of *Otonycteris* have high and sharp cones, well-developed and sharp crests of the buccal stylar shelf (ectoloph) and sharp pre- and postprotocrista. The main cones and ectoloph cuspids (para-, meso- and metastyle) of the upper molars are located towards the protocone and close to the center of the crown. The M2 is less elongated in the buccolingual direction and both the M1-2 have neither paraconule and paraloph nor metaloph. The lower incisors are similar in size and stand very close to each other, so that the incisor-row is relatively thick. Besides these peculiarities, the dentition of *Otonycteris* is strongly reduced: there is only one upper incisor I1, the I2 is lost, the upper small premolars are reduced as is also the p3. In addition some teeth crowns are strongly reduced: the M3 has a short paracrista, the metacone is lost, and moreover, the protocone of M3 is appreciably reduced; the talonid of m3 is also reduced in size and often has no hypoconulid. On the other hand, all the teeth of *Otonycteris* have a well-developed cingulum, which in the lower molars forms the entocingulid at the foot of the trigonid valley on the anterolingual base of the metaconid. Besides, *Otonycteris*, *Antrozous pallidus* Le Conte, 1856*, Histiotus montanus* Philippi & Landbeck, 1861, *Ia io* Thomas, 1902*, Hesperoptenus (Milithronycteris) blanfordi* Dobson, 1877, and some large *Myotis* (e.g. *M. myotis*; Fig. 4) have the entocingulid, which is present in a different degree of development in all of these recent bats. Apparently, the Australian *Nyctophilus bifax* Thomas, 1915 has also an entocingulid in lower molars in agreement with the illustrations in Martinez (2010: 104, Fig.

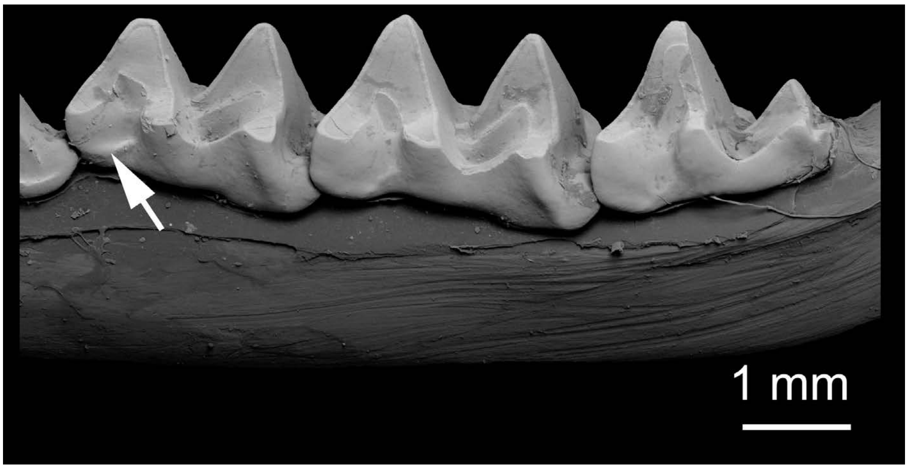

Figure 4. *Myotis myotis,* S-103165, coll. ZMMU; lower molars with weak entocingulid **(**marked by the white arrow sign**)**, ventral view.

3.32). But both the fossil *O. rummeli* and *Karstala silva* have the most developed entocingulid in the lower molars.

It seems to be evident that different dental traits may have evolved in association with diet and that dietary ecology shaped the evolution of molar morphology (Hunter & Jernvall, 1995). Moreover, tooth morphology can have an effect on an animal's nutrient intake and digestibility and thus strong selective pressures should act on tooth shape and function (see references in Santana *et al.*, 2011). Thus, odontological morphology of *Otonycteris* should reflect peculiarities of its diet and trophic ecology.

It is known that *Otonycteris* species forage either very close to the ground or at the height of some 4-8 metres (Horáček, 1991; Arlettaz *et al.*, 1995; Fenton *et al.*, 1999; Korine & Pinshow, 2004; Daniel *et al.*, 2008). They glean arthropods from ground, rock, and plant surfaces and their prey includes mainly large ground Coleoptera, Blattodea, Orthoptera, Solpugida, and Scorpionida (Horáček, 1991; Arlettaz *et al.*, 1995; Benda & Gvoždík, 2010; Holderied *et al.*, 2011). Freeman (1979, 1981) suggested that bats consuming hard-shelled prey items (e.g. beetles) have larger teeth and heavier, shorter jaws than those eating primarily soft-shelled items (e.g. moths). The beetle eaters, among other things, are characterized by a relative long upper canine and a relative thick dentary. In addition, larger bats tend to eat larger prey (Freeman & Lemen, 2007). Obviously, the function of the large canines of *Otonycteris* is to grasp prey and to kill the large and hard-shelled prey, whether it is invertebrate or vertebrate in nature. They are intimately involved in the initial break up of food, which is processed by the large postcanine teeth.

Given that an early evolutionary trend in bats is brachycephaly, initiated by the simplification (demolarization) and reduction in number of the premolars (Slaughter, 1970), the initial stage in the evolution of bat dentition may be characterized by a long rostrum of skull with maximally long tooth rows and a full number of premolars (Tate, 1942). If true, it is probable that the robust skull of *Otonycteris* with well-developed cranial crests, thick jaws and fewer, larger teeth are evidently derivative features, whereas a relatively elongated skull with comparatively long rostrum a primitive character.

The developed cingulum of bat dentition fills in the space between the teeth, the interdental embrasure, eventually squaring off these teeth. It serves as a guard, protecting the periodontal tissue from damage by fragmented insect exoskeletons (Slaughter, 1970). The well-developed entocingulid in both the *Otonycteris* and *Antrozous pallidus* is not involved in occlusion so that it remains intact and also has no occlusion marks in specimens with much worn tooth crowns (e.g. specimen SMF 19427). Thus, the entocingulid in these bats apparently has mostly the function of protection.

Morphologically, *O. rummeli* is most similar to recent *Otonycteris* species but it differs in being larger and in having a more developed entocingulid that may be evidence of the presence of larger and harder-shelled prey in its diet. Recent *O. hemprichii* sensu stricto is considered the strongest predator among Palearctic insectivorous bats. As such, the larger fossil *O. rummeli* must be considered a strong predator as well. Further it differs from recent *Otonycteris* species in having the shallow concavities of the anterolingual and posterolingual faces of the upper canine crown which are deeper in recent species (Fig. 3 A, B) and a less developed anterobuccal ridge of the crown. These features together with a clearly defined mesolingual cingular cuspid in the upper canine crown of *O. rummeli* apparently also could be considered as a more primitive feature in comparison to the recent *Otonycteris*.

Phylogenetic considerations

According to the modern molecular, morphological and karyological investigations, the close phylogenetic relationship of *Otonycteris* to the members of the Plecotine tribe appears clear (Hill & Harrison, 1987; Horáček, 1991; Zima *et al.*, 1992; Qumsiyeh & Bickham, 1993; Bogdanowicz *et al.*, 1998; Benda & Gvoždík, 2010). Moreover, recent *Otonycteris* is morphologically the most divergent of all Plecotini, considering morphologic and genetic characteristics (Bogdanowicz & Owen, 1996). However, according to an alternative point of view *Otonycteris* is not a member of the Plecotine tribe (e.g. Frost & Timm, 1992) and until quite recently, this genus was considered to be either a member of Nycticeiini (Koopman, 1994; McKenna & Bell, 1997) or Eptesicini (Menu, 1987). Based on the mtDNA sequence data, Hoofer & Van Den Bussche (2001) suggested a close relationship between *Otonycteris* and *Antrozous* from North America. Their arrangement agrees also with phallus morphology (Pine *et al.*, 1971) and morphologic and karyotypic data (Horáček, 1991; Zima *et al.*, 1992) supporting the close association of these two genera. However, recent phylogenetic analyses of molecular data clearly support *Otonycteris* as a member of the tribe Plecotini and independent position of *Antrozous*, which forms a supported clade with *Rhogeessa* in all phylogenies, what lends support to the tribe Antrozoini (Roehrs *et al.,* 2011). Nevertheless, the wing parameters of *Otonycteris* are similar to *Antrozous* (Norberg & Fenton, 1988) and these genera show some similarities in trophic niche (Arlettaz *et al.*, 1995; Freeman, 1998). *Antrozous pallidus* shows a large geographical variation in dietary composition, but scorpions and even small vertebrates (the silky pocket mice *Perognathus*) are taken, although both generally represent a minor proportion of the diet (Bell, 1982; Orr, 1954; O'Shea & Vaughan, 1977). As discussed above, *O. hemprichii* gleans arthropods and its prey includes also Solpugida and Scorpionida (Horáček, 1991; Arlettaz *et al.*, 1995; Benda & Gvoždík, 2010). Some captive individuals of *O. hemprichii* show the behaviour of carnivores, as they were able to eat geckos (Gorelov, 1977 in Horáček, 1991). In our comparison of dentitions of these two species, *Otonycteris* also shares morphological similarities with *Antrozous*. First of all, both have well-developed entocingulids in the lower molars, which is also well-developed in the lower molars of another North American fossil species *Kastala silva* from the Early Miocene of Florida.

Old and New World bat faunal interchanges and paleogeographic implications of new *Otonycteris* fossil records

In the discussion of possible phylogenetic relationships among *Otonycteris*, *Antrozous* and *Karstala* the questions about the center of bat origin and faunal interchanges between Old and New Worlds cannot be ignored. The question about the center of Chiropteran origin is still being debated. Some recent studies suggest a Laurasian origin for bats, possibly in North America during the early Paleocene (Cracraft, 1973; Hand, 1984; Teeling *et al.*, 2005). Others support a Southern Hemisphere origin of modern-day bat families in Africa (Sigé, 1991; Springer *et al.*, 2003; Teeling *et al.*, 2003; Delsuc *et al.*, 2004; Eick *et al.*, 2005). It is generally accepted that modern bats were already well diversified and had a widespread distribution as early as the early Eocene (Smith *et al.*, 2007, 2012; Ravel *et al.*, 2014). The timing of diversification in the late Paleocene-early Eocene coincides both with the late Paleocene thermal maximum and early Eocene climate optimum, that is, the late Paleocene-early Eocene global warming interval (Zachos *et al.*, 2001). In the middle Eocene there was a progressive cooling and drying trend, with tropical rainforests on the decline around the world (Prothero, 1994). In the Eocene the terminal stages of the separation of North America from Europe by the North Atlantic Ocean took place, and the final separation apparently had taken place by about 47-49 Myr (see references in Cracraft, 1973). South America and Africa had been split from each other by the South Atlantic Ocean earlier, between 100-84 Myr (Eick *et al.*, 2005). So, up to the mid-Early Cretaceous fauna interchange between Old and New Worlds was possible via direct connection between South America and Africa (ibid.).

The early Eocene was a time of maximal fauna interchanges between the Old and New Worlds (Janis, 1993; Prothero, 1994). At this time, island hopping when sea levels were low or rafting across large water barriers would have been the only possible modes of dispersal between South America and Africa (Parrish, 1993). Such dispersal between Africa and South America was possible even for terrestrial mammals, e.g. for monkeys and caviomorph rodents (see references in Eick *et al.*, 2005; Flynn & Wyss, 1998; Antoine *et al.*, 2014; Bond *et al.*, 2015). In the Eocene it is plausible that a northwards dispersal of mammals occurred from Africa to Eurasia across the Tethys Sea and then with entry into North America accomplished via Beringia or over transatlantic land bridges via Greenland (Janis, 1993; Sanmartin *et al.*, 2001; Cox, 2001). North America and Asia were linked intermittently throughout the Cenozoic by Beringia, and terrestrial connections between Europe and North America persisted along various North Atlantic land bridges until at least the early Eocene (50 Ma) (see references in Eick *et al.*, 2005). Dispersal of mammals between North and South America could then have occurred via the proto-Caribbean archipelago, which connected these continents from 100 to about 49 Ma, by means of island hopping (Sanmartin & Ronquist, 2004) or direct flight in the case of bats (Eick *et al.*, 2005).

Using both morphological and molecular methods Eick *et al.* (2005) concluded that two intercontinental dispersal events, from Africa to either North America or South America in the early Eocene, explain the presence of the ancestor of the superfamily Noctilionoidea and family Natalidae in the Americas. Based on the new paleontological data Gunnell *et al.* (2014) proposed that the origins of Noctilionoidea may be found in eastern Gondwana with a subsequent dispersal into Australia and then on to South America across Antarctica.

Evidence for movement of bats between the Old and New Worlds after the Eocene is limited but some exists. For instance, some new molecular studies of the genotypes of a blood parasite, *Trypanosoma dionisii*, in Old World bats has shown that they are closely related to South American strains (Hamilton *et al.*, 2012). The authors suggest that movement of bats between the Old and New Worlds within the last ca. 5 million years, certainly since geographical isolation of the Old and New Worlds, is the most likely explanation for the observed distribution of these trypanosomes (ibid.). Thus, it seems that bats can disperse trypanosome genotypes across substantial geographical barriers. It was also proposed that *Tadarida* and *Mormopterus* may have emigrated to North America from Eurasia across the Bering land bridge in the early Miocene or before, and then immigrated into South America in the late Pliocene (Czaplewski *et al.*, 2003).

Phylogenetic evidence supports a monophyly of the New and Old Worlds *Myotis* and a Palaearctic origin for the ancestors of the New World clade, which was separated from the Old World taxa during the Miocene (*ca.* 12.2 ± 2.0 Myr) and reached the New World via the Bering Strait (Stadelmann *et al.*, 2007). The global decline in temperature and drop in sea levels at the Middle Miocene (Zachos *et al.*, 2001; Böhme, 2003) correspond to the first major periods of mammalian immigrations via the Bering land connection between Siberia and Alaska in the Middle Miocene (Wolfe, 1994).

Based on phylogenetic evidence and current geographic distributions of recent and fossils species the Plecotine tribe probably originated in the eastern Hemisphere (Bogdanowicz *et al.*, 1998). Recent species of *Corynorhinus* are currently restricted to the Nearctic and *Plecotus* species are limited to the Palaearctic (ibid.). However, remains of *Corynorhinus* are known from the upper Miocene of Hungary (Polgárdi, MN 13; Topal, 1989). Moreover, some *Plecotus*-forms that in cranial morphology resemble the Nearctic *Corynorhinus* are described from the Late Miocene of Austria (Kohfidisch, MN 11; Rabeder, 1973) and from the Plio-pleistocene sites of Poland, Hungary and Austria (Podlesice, Osztramos Loc. 9, Deutsch-Altenburg 2, Beremend Loc. 17; Kowalski, 1956; Wołoszyn, 1987; Rabeder, 1974; Topal, 1989). Topal (1989: 53) hypothesized that *Corynorhinus* occurred in Eurasia as early as ca. 6 Myr and that it disappeared from Europe during the Betfian substage of the lower Pleistocene. Later it was assumed that North America was invaded by a plecotine bat at least twice, probably first by *Corynorhinus* species and then later by a more *Plecotus*-like ancestor of the highly derived *Euderma-Idionycteris* clade (cf. Bogdanowicz *et al.*, 1998). Thus, the bat faunal interchange between the Old and New Worlds apparently occurred in the Paleogene and Neogene.

On the other hand, there are strong suggestions that the geographic separation of the Old and New Worlds has been an effective barrier to the distribution of bats (Hamilton *et al.*, 2012). High endemism exists at each taxonomic level of each biogeographical region (Teeling *et al.*, 2005) and the global distribution of bat taxa indicates that the Atlantic and Pacific Oceans are effective barriers to faunal exchanges between the Old and New Worlds. For instance, one of the major suborders, Yinpterochiroptera, has an exclusively Old World distribution, and within the other, Yangochiroptera, no species and only five genera are common to both the Old and New Worlds (cf. Hamilton *et al.*, 2012).

The bat radiation remains enigmatic and complex, but evidently it is closely related to the active flight of bats and to the migration abilities of modern bats. Recent bats are the only flying mammals to exhibit true seasonal return migrations, broadly defined as long-distance migrations (classified as moving more than 1000 km, but in practice between 1000 and 2000 km) and short-distance migrations (classified as moving in practice between 100 and 600 km; data from Fleming & Eby, 2003, Hutterer *et al.*, 2005 with the correction of Bisson *et al.*, 2009). Two types of migrations of bats have evolved independently in several lineages, potentially as a strategy to exploit seasonal resources, acquire higher quality hibernating and/or breeding habitat, and to potentially avoid predators or disease (cf. Bisson *et al.,* 2009). Most of the migratory species belong to the family Vespertilionidae, which are exclusively insectivorous and inhabit temperate zones (Bisson *et al.,* 2009).

Apparently the long-distance migrations of bats are related to their worldwide distribution. Some bats were apparently blown off-course by more than 1000 km during migrations (see references in Constantine, 2003) and were able to colonise isolated islands, implying natural movement over a distance of over 4000 km (Morales & Bickham, 1995). Thus, occasional natural migrations of bats between the New and Old Worlds do appear to be possible, but it is a relatively rare phenomenon (Bisson *et al.,* 2009). Less than 3% of extant bat species show migratory movement of any kind with less than 0.016% of extant bat species moving over 1000 km in a one-way journey (Fleming & Eby, 2003). For example, some narrow stretches of open water (> 14 km) can be absolute barriers, e.g. for *Myotis* bats, which otherwise are wide ranging over terrestrial landscapes (cf. Castella *et al.*, 2000). But occasionally, some New World bats, such as *M. lucifugus*, have been accidentally transported on board ships to Europe (Constantine, 2003).

In light of the comments above-mentioned, it seems that the bat faunal interchanges between the New and Old Worlds may have occurred in the Paleogene and Neogene but they were relatively rare. The same is true with respect to the intercontinental migratory dispersion of recent bats. It is more likely that bat faunas of the Old and New Worlds, since the time of their geographic separation, in general evolved independently. Accordingly, it is unlikely that the morphological resemblance of the Ukrainian *Otonycteris* and New World species *Karstala* and *Antrozous* reflect a close phylogenetic relationship but it is probably the result of parallelism. The array of dental characteristics within the family Vespertilionidae seems to be rife with parallelisms and often does not reflect the phylogenetic grouping, but rather represents adaptive convergences that produced the same ectomorphs independently through deterministic processes. Such evidence of convergent or parallel evolution of characteristics, and of the strong influence of geographic origins of species in shaping phylogenetic relationships is now supported by a growing number of molecular studies (e.g. Ruedi & Mayer, 2001; Roehrs *et al.*, 2011).

Taphonomical and paleoclimatic considerations

The Gritsev site is a fissure filling in reef-forming limestones, thus the taphocenosis has a karstic genesis (Rosina & Semenov, 2012). Two factors – the natural death of the animals living in rock fissures and raptor pellets – most probably codetermined the bone accumulation and their subsequent fossilization in such localities. Recent species of *Otonycteris* roost in both the cracks of rocks (Shai, 2005; Shai *et al.*, 2008, 2010 a, b; Korine *et al.*, 2013) and in human constructions (Gharaibeh & Qumsiyeh, 1995; Harrison & Bates, 1991 in Fenton *et al.*, 1999), mostly solitary or up to 18 females during breeding (Bogdanov, 1953 in Gharaibeh & Qumsiyeh, 1995; Shai *et al.*, 2008). In addition, remains of this bat were frequently found in owl pellets in Algeria (Heim de Balsac, 1965), Syria (Shehab *et al.*, 2004) and Israel (Tores & Yom-Tov, 2003). Thus, it is quite natural that the remains of *Otonycteris* have been found at the Gritsev taphocenosis.

At present, the genus *Otonycteris* is a Saharo-Sindian faunal element which inhabits arid and semiarid areas of the central and southwestern Palaearctic from Morocco, Southern Algeria and Niger to Egypt and Sudan and the whole Middle East and Central Asia to Afghanistan and Northwestern India (Benda & Gvoždík, 2010: 84, Fig. 1). However, judging by the finds of this genus in La Grive M (MN 7, France; Mein & Ginsburg, 2002), from at least the Middle Miocene the range of *Otonycteris* distribution had spread apparently to the whole of Central Europe. Such a situation had continued during the whole Late Miocene as proved by the finds of *O. rummeli* nov. sp. in Gritsev (MN 9, Ukraine) and also *Otonycteris* sp. in Soblay (MN 10, France; Ménouret & Mein, 2008). If we suggest that climatic requirements for this ancient *Otonycteris* were perhaps as restrictive as they are today for recent *Otonycteris* species then we can propose a more arid climate in Europe in the Upper Miocene compared to the Quaternary. It is generally accepted that at the beginning of the Late Miocene the climate of Southeastern Europe become more arid and slightly colder (van Dam, 2006; Brayard *et al.*, 2004; Syabray *et al.*, 2007) in accordance with a general climatic cooling trend, which starts in Europe at *ca.*14 Myr (Utescher *et al.*, 2000; Mosbrugger *et al.*, 2005). This process was followed by fluctuations of palaeoclimate parameters and display cyclic changes of humid/dryer and warmer/cooler conditions (Ivanov *et al.*, 2011), which are recorded for the Ukraine Plain up to ca. 7.5 Myr (Syabray *et al.*, 2007; Ivanov *et al.*, 2011). The global warm climate during the Early Pliocene was impacted by a major change into a global cooling, related to the Northern Hemisphere Glaciation at *ca.* 2.6 Myr between the Middle and Late Pliocene (Lisiecki & Raymo, 2007; also see references in Popescu, 2008). Long-term trends of climatic cooling and increasing glacial cycle amplitude during the Plio-Pleistocene are apparently also suggestive of significant changes in terrestrial biota. Such climate changes could be a probable cause for the reduction of the distribution range of *Otonycteris* and its extinction in most of the territory of Europe.

CONCLUSION

The Late Miocene new species of the rare genus *Otonycteris* from the Ukraine shows a strong morphological resemblance with New World bat species *Antrozous* and *Karstala* and apparently is more evidence of convergent and independent evolution in Old and New World bat faunas that produced the same ectomorphs independently through deterministic processes. Together with the Late Miocene records of *Otonycteris* from France (La Grive M, MN 7 and Soblay, MN 10) these new fossils from the Ukraine are helpful for climatic reconstruction in the Late Miocene of Europe. From at least the Middle Miocene the range of *Otonycteris* distribution had spread apparently to the whole of Central Europe and such a situation continued during the whole Late Miocene. It indicates a more arid climate in Europe during the Upper Miocene compared to the Quaternary. The reduction of the distribution range of *Otonycteris* and its extinction in most of the territory of Europe could have been caused by the global climatic cooling and increasing glacial cycle amplitude with the onset of the Quaternary.

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